Thelastoma dessetae n. sp. (Thelastomatoidea; Oxyurida; Nematoda) from Paraguayan diplopods with comments on reproductive anatomy in Thelastoma

by

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With 1 figure

ABSTRACT

Thelastoma dessetae n. sp. is described on the basis of females from Rhinocricus bernardinensis (Rhinocricidae; Diplopoda) from near the border of Paraguay and Argentina. A list of nominal species of Thelastoma is given. The new species is distinguished from other known species on the basis of the body cuticle anterior to the first annulation; this forms a truncate cone extending to well posterior to the beginning of the oesophagus in T. dessetae but forms a short circum-oral ring extending at most to the level of the base of the buccal cavity in other Thelastoma spp. T. dessetae is didelphic but a seminal receptacle is absent on the anterior branch of the reproductive tract; eggs produced in this branch are unfertilized whereas those produced in the posterior branch are fertilized. It is suggested that this phenomenon is widespread in Thelastoma and represents an adaptation to haplodiploidy. Haplodiploids must produce a mixture of fertilized and unfertilized eggs to ensure male and female progeny.

INTRODUCTION

COBB (1929) noted that in certain didelphic thelastomatoids (Oxyurida; Nematoda), a seminal receptacle was present on only one of the reproductive horns. He interpreted this as an instance of hermaphroditism (the actual term he used was "syngony") and proposed this as an explanation for the rarity of males in the Oxyurida.

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Recently (see ADAMSON 1984 for a review) we showed that the Oxyurida reproduce by haplodiploidy, i.e., males develop from unfertilized eggs and are haploid whereas females develop from fertilized eggs and are diploid. We interpreted the absence of a seminal receptacle on the anterior horn of the reproductive tract of the thelastomatoid *Desmicola skrjabini* as an adaptation assuring a certain number of unfertilized eggs, and therefore male progeny, in each generation.

Thelastoma dessetae n. sp. from Rhinocricus bernardinensis (Rhinocricidae; Diplopoda) from Paraguay lacks a seminal receptacle on the anterior horn of the female reproductive tract and therefore gave us an opportunity to further examine the significance of this feature.

MATERIALS AND METHODS

Two specimens of *Rhinocricus bernardinensis* (identification made by Dr. J. P. Mauriés and Professor J. M. Demange, Laboratoire des Arthropodes, Muséum national d'Histoire naturelle, Paris) collected in the region of the Iguassu Falls during the zoological expedition of the Geneva Museum of Natural History to Paraguay in 1982, were fixed in 70% ethanol. Nematodes collected from the posterior intestine were stored in 70% ethanol before being cleared and studied in lactophenol. The material consists of three females stored in the parasite collection of the Paris Museum of Natural History (Laboratoire de Zoologie — Vers: Type, KP 160; other specimens, KP 159).

DESCRIPTION OF MATERIAL

Thelastoma dessetae n. sp.

General Description:

Relatively stout worms with blunt cephalic extremities. Body gradually increasing in width posteriorly, reaching maximum width just behind level of vulva, abruptly rounded posterior to anus and supporting filiform caudal appendage.

Body cuticle bearing distinct annulations. Cuticle anterior to first annulation forming truncate cone extending well posterior to level of anterior extremity of oesophageal corpus. Annules increasing gradually in width posteriorly and becoming indistinct posterior to anus.

Oral opening triradiate. Lips absent. Cephalic sense organs consisting of four submedian pairs of outer papillae, six inner papillae just inside buccal cavity and two amphids. Anterior portion of buccal capsule a sclerotized cylinder, its lumen triradiate in apical view; posterior portion with one dorsal and two subventral pennate cuticular projections at its base. Corpus subcylindrical, tapering slightly just before isthmus. Isthmus not sharply demarcated from corpus. Excretory pore just posterior to level of junction of isthmus and bulb. Two pairs of coelomocytes present on ventral side: one pair just posterior to oesophageal bulb and one pair just anterior to vulva.

¹ Expedition in collaboration with 'la Cooperation technique Suisse' and the 'Inventario biologico di Minestario de Agricultura y Granaderia, Paraguay'.

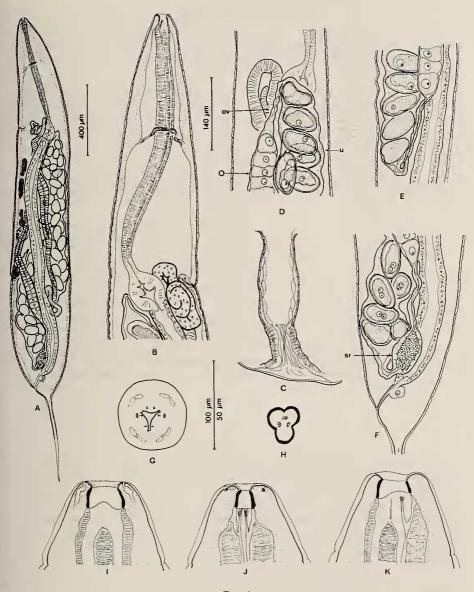


Fig. 1.

Thelastoma dessetae n. sp., holotype female except E, an uninseminated female.

A, entire worm, left lateral view. B, oesophageal region, right lateral view. C, vulva and vagina, ventral view. D, anterior extremity of reproductive tract: ovary = O; oviduct = ov; uterus = u. E, posterior extremity of reproductive tract of uninseminated female: note absence of seminal receptacle. F, posterior portion of reproductive tract of inseminated female: seminal receptacle = sr. G, superficial apical view. H, section through buccal capsule. I to K, cephalic extremity: I, dorsal view; J, ventral view; K, lateral view.

Scales: $A = 400 \, \mu m$ scale; B, and D to $F = 140 \, \mu m$ scale; $C = 100 \, \mu m$ scale; G to $K = 50 \, \mu m$ scale.

Reproductive Anatomy:

Reproductive tract consisting of paired ovaries, oviducts and opposed uteri, and common vagina. Vagina directed anteriorly from vulva, divided into muscular and glandular portions.

Holotype: One ovary, its blind end coiled on right side of oesophageal bulb, extending posteriorly on left side of body to join oviduct; oviduct leading through prominent oblong seminal receptacle to anteriorly directed uterus. Other ovary, its blind end coiled on right side of intestine in posterior part of body, extending anteriorly on right side to join oviduct near posterior extremity of oesophagus; oviduct leading directly to posteriorly directed uterus (no seminal receptacle present).

Eggs in utero (approximately 60 in number) developed only as far as pronuclear stage. Thirty eggs in pronuclear stage in posterior uterus, all with two pronuclei; twenty-one eggs in pronuclear stage in anterior uterus, all with single pronucleus.

Other specimens: Position of ovaries as in holotype. Spermatozoa and seminal receptacle absent in both reproductive horns; all eggs in utero with single pronucleus.

Dimensions (Holotype followed by two specimens in parentheses): Length 2.47 (1.71, 2.40) mm. Maximum width 243 (120, 200) μm just posterior to vulva. Buccal capsule 15 (14, 17) μm long. Oesophagus 657 (536, 650) μm long, consisting of corpus 520 (433, 518) μm and isthmus 52 (35, 43) μm long, and bulb 85 (68, 89) μm long and 78 (69, 86) μm wide. Nerve ring 250 (227, 250) μm, excretory pore 584 (470, 581) μm and vulva 1.37 (0.97, 1.30) mm from anterior extremity. Vagina 165 (158, 172) μm long: muscular portion 67 (70, 77) μm and glandular portion 98 (88, 95) μm long. Annulations beginning 42 (53, 49) μm from anterior extremity, 16 (10, 13) μm apart in oesophageal region and 25 (14, 17) μm apart just anterior to anus. Tail 548 (376, 597) μm long. Eggs 44-55 m wide and 85-92 μm long (11 eggs measured from the three specimens).

SYSTEMATIC COMMENTS AND DIAGNOSIS

Thelastoma is among the most problematic of thelastomatoid genera mainly because of the large number of inadequately known species. BASIR (1956) and LEIBERSPERGER (1960) outlined the taxonomic history of the genus and attempted to clarify the status of the known species. KLOSS (1965) listed 17 taxa but considered only six of these as valid species. JARRY & JARRY (1968) recognized three valid species and listed 19 synonyms, three species inquirenda and two species which they classified as indeterminable. Although synonyms are likely to exist among the forty or so nominal species of Thelastoma, such extensive synonymization, based uniquely on published descriptions, is imprudent, especially since many of the proposed synonymies involve taxa occuring in different host groups and geographical regions. We give the following uncritical list of Thelastoma spp. arranged by host group:

DIPLOPODA

— T. attenuatum Leidy, 1849 (= Aorurus (Thelastoma) attenuatum Leidy) from Julus (s. l.) marginatus in eastern USA.

Comments: type species, male undescribed.

— T. labiatum Leidy, 1850 (= Aorurus (Thelastoma) labiatum Leidy) from Polydesmus virginiensis from eastern USA.

Comments: male undescribed.

T. pachyjuli (Parona, 1896) Travassos, 1929 (= Oxyuris pachyjuli Parona) from Julus (s. l.) communis from Palermo, Sicily.

Comments: male undescribed.

- T. longicaudata (Meyer, 1896) Travassos, 1929 (= Oxyuris longicaudata Meyer) from Julus (s. l.) sp. from Sri Lanka.
 Comments: male undescribed.
- T. platyrhaci (Parona, 1896) Skrabin, Schikhobalova and Lagodovskaya, 1966
 (= Oxyuris platyrhaci Parona) from Platyrhacus modiglianii from Sumatra.
 Comments: male undescribed.
- T. myriapodicola (Skrjabin, 1916) Skrjabin, 1923 (= Oxyuris myriapodicola Skrjabin;
 = Johnstonia myriapodicola (Skrjabin) Basir, 1956) from Polydesmus sp. from East Africa.

Comments: male undescribed.

T. crimense Skrjabin, 1927 (= Johnstonia crimense (Skrjabin) Basir, 1959) from Julus
 (s. l.) sp. from Caucasia and Crimea, USSR.

Comments: male undescribed.

- T. myolabiatum Cobb, 1929 from Fontaria marginata from Virginia, USA.
 Comments: male undescribed.
- T. spicatum Cobb, 1929 from Spirobolus marginatus from eastern USA.
 Comments: male undescribed.
- T. pteroton Dollfus, 1952 from Julus (s. l.) sp. from the Ivory Coast.
- T. indica Rao, 1958 from Spirostreptus sp. from Hyderabad, India.
- T. bulhoesi dollfusi Ruiz and Coelho, 1955 from Neptunobolus hogei from São Paulo, Brazil.

Comments: male undescribed.

- T. dollfusi Osche, 1960 from a Spirostreptinae from Africa.

Comments: male undescribed.

- T. ornata Singh, 1955 from Thyroglutus malayus from Lucknow, India.
- T. rovinjense Leibersperger, 1960 from Pachyjulus fusipes from Jugoslavia.
- T. delphyhystera Dollfus, 1964 from Plagiodesmus occidentalis tuberosus from the Congo.

Comments: male undescribed.

- T. nasuta Kloss, 1965 from Heterostreptus coeruleopes from Para, Brazil.
- T. paronai Kloss, 1965 from Dicranostreptus restingae from Rio de Janeiro state, Brazil.

BLATTOIDEA

T. bulhoesi (Magalhaes, 1900) Travassos, 1929 (= Oxyuris bulhoesi Magalhaes;
 = Bulhoesia bulhoesi (Magalhaes) Schwenck, 1926) from Periplaneta americana from Brazil.

Comments: type of *Bulhoesia* Schwenck, 1926. CHITWOOD (1932) redescribed the female and described the male from North American *Periplaneta americana*.

 T. icemi (Schwenck, 1926) Travassos, 1929 (= Bulhoesia icemi Schwenck) from wild Blattidae from São Paulo State, Brazil.

Comments: male undescribed.

- T. riveroi Chitwood, 1932 from Periplaneta sp. from Cuba.
- T. palmettum Chitwood and Chitwood, 1933 from Panesthia javanica from the Philippines.

Comments: male undescribed.

- T. aligarhica Basir, 1940 from Periplaneta americana from Aligarh, India.
- T. thapari (Singh and Singh, 1958) Kloss, 1965 (= Bulhoesia thapari Singh and Singh) from Periplaneta americana from Lucknow, India.
- T. blabericola Leibersperger, 1960 from Blaberus cranifer and Blaptica dubia from Germany.
- T. periplaneticola Leibersperger, 1960 from Periplaneta americana from Germany.
- T. madecassa van Waerebeke, 1969 from Elliptoblatta madecassa from Madagascar.
- T. pachyjuli tampoketsii van Waerebeke, 1969 from Blatta sp. from Madagascar.
- T. malaysiense Anuar and Paran, 1977 from Periplaneta americana from Malaysia.

COLEOPTERA

- T. robustum Leidy, 1850 (= Aorurus (Thelastoma) robustum Leidy; = Schwenkiella robustum (Leidy) Basir, 1956) from unidentified larval coleopteran from eastern North America.
 - Comments: redescribed by Christie (1938).
- T. alatum Johnston, 1914 (= Johnstonia alata (Johnston) Basir, 1956) from larval Cetonidae from North Queensland, Australia.
 - Comments: type of Johnstonia Basir, 1956.
- T. macramphidum Christie, 1931 from larval Osmoderma sp. (Scarabaeidae) from Michigan, USA.
- T. papilliferum Christie, 1931 from larval Osmoderma sp. from Michigan, USA.
 Comments: Christie (1938) considered this species a synonym of T. macramphidum.
- T. toxi van Waerebeke, 1970 from larval Figulus sublaevis and Prosopocoelus serricornis (Lucanidae) from Madagascar.
- T. figuli van Waerebeke, 1970 from larval Figulus sublaevis from Madagascar.
- T. patella van Waerebeke, 1970 from adult Hexodon patella and H. latissimum (Scarabaeidae) from Madagascar.
- T. unicoloris van Werebeke, 1970 from adult Hexodon unicolor from Madagascar.
- T. pyrrhus van Waerebeke, 1973 from larval Oryctes pyrrhus (Cetonidae) from Madagascar.
- T. mamba van Waerebeke, 1973 from larval Oryctes sp. from Madagascar.
- T. ritteri van Waerebeke, 1973 from larval Oryctes politus from Madagascar.
- T. pterygoton Poinar, 1973 from larval Oryctes sp. from the Ivory Coast.

OLIGOCHAETA

- T. endoscolicum Poinar, 1978 from Eudrilus eugeniae from the Ivory Coast.

Many of the above forms are poorly known and it is difficult to compare them with our material for many details. Below is a list of the principal distinguishing characters of *T. dessetae* n. sp., followed by a list of species sharing the character and, where applicable, a list of species for which the character cannot be assessed.

— 1. — Cuticle anterior to first annulation forming truncated cone which extends well posterior to beginning of oesophagus.

In all other *Thelastoma* spp., the lip region forms a short terminal annule extending at most to the base of the buccal capsule.

2. — Isthmus of oesophagus only lightly demarcated from corpus.

Character shared by T. pteroton and T. indica.

- 3. - Anterior extremely of intestine narrower than bulb.

Character shared by T. longicaudata.

4. — Buccal capsule with one dorsal and two subventral pennate cuticular projections at its base.

Character shared by *T. palmettum*; in a number of other species there are knob-like teeth at the base of the buccal capsule. Character cannot be assessed in *T. attenuatum*, *T. labiatum*, *T. pachyjuli*, *T. longicaudata*, *T. platyrhaci*, *T. myriapodicola*, *T. crimense*, *T. myolabiatum*, *T. spicatum*, *T. indica*, *T. bulhoesi dollfusi*, *T. ornata*, *T. delphyhystera*, *T. icemi*, *T. bulhoesi*, *T. riveroi*, *T. aligarhica*, *T. malaysiense*, *T. robustum* and *T. alatum*.

- 5. - Oesophagus long, over 20% of body length.

Character shared by T. attenuatum, T. pteroton, T. indica, T. bulhoesi dollfusi, T. bulhoesi, T. riveroi and T. palmettum. Character cannot be assessed in T. labiatum, T. myolabiatum and T. spicatum.

— 6. — Excretory pore just posterior to level of junction of oesophageal isthmus and bulb.

Character shared by T. pachyjuli, T. myriapodicola, T. rovinjense, T. ornata, T. riveroi, T. bulhoesi, T. alatum, T. madecassa, T. papilliferum, T. pyrrhus, T. patella and T. endoscolicum. Character cannot be assessed in T. longicaudata, T. platyrhaci, T. spicatum and T. delphyhystera.

- 7. - Tail short, less than 25% of body length.

Character shared by T. myriapodicola, T. spicatum, T. myolabiatum, T. dollfusi, T. icemi, T. thapari, T. blabericola, T. madecassa, T. toxi, T. pyrrhus, T. patella, T. unicoloris, T. endoscolicum and T. pterygoton.

SIGNIFICANCE OF THE REPRODUCTIVE ANATOMY OF THELASTOMA

This is only the second report of a single seminal receptacle in a species of *Thelastoma*. However, the phenomenon is almost certainly more widespread since VAN WAEREBEKE'S (1969, 1970a, b, 1973) illustrations suggest it occurs in all Madagascan species; POINAR (1973) clearly illustrates a single seminal receptacle in *T. pterygoton*. In all instances, it is the anterior reproductive horn which lacks a seminal receptacle.

The present observations on *T. dessetae* support our 1983 hypothesis explaining the absence of a seminal receptacle on the anterior reproductive horn of the thelastomatoid *Desmicola skrjabini*. Thelastomatoids, being haplodiploid, must produce a mixture of fertilized and unfertilized eggs to ensure both sexes among their progeny. In the inseminated female of *T. dessetae*, eggs in the anterior horn contained a single pronucleus indicating that they had not been fertilized and presumably would have developed as males. Eggs in the posterior horn contained two pronuclei; they had thus been fertilized and presumably would have developed as females.

The presence of unfertilized eggs in *T. dessetae* indicates that males probably exist and that COBB'S (1929) hypothesis of hermaphroditism does not apply. However, hermaphroditic reproduction and haplodiploidy are not incompatible. Thus, in the haplodiploid coccoid, *Icerya purchasi*, hermaphrodites develop from fertilized eggs; oogonia are diploid whereas spermatogonia are haploid (HUGHES-SCHRADER 1927).

Uninseminated female *T. dessetae* had no seminal receptacle; their uterine eggs contained a single pronucleus. Two possibilities exist:

- (1) the females are uninseminated haplodiploids and their uterine eggs would have developed as males; sperm may be neccessary for the development of the seminal receptacle,
- (2) the females represent a parthenogenetic strain and their eggs would have developed as parthenogenetic females.

BIBLIOGRAPHY

- Adamson, M. L. 1983. Anatomical adaptation to haplodiploidy in the oxyuroid (Nematoda) *Desmicola skrjabini* n. sp. from a diploped in Gabon. *Annls Parasitol. hum. comp.* 59:95-99.
 - 1984. L'haplodiploïdie des Oxyurida. Incidence de ce phénomène dans le cycle évolutif. Annls Parasitol. hum. comp. 59: 387-413.
- BASIR, M. A. 1956. Oxyuroid parasites of arthropods. A monographic study. 1. Thelastomatidae. 2. Oxyuridae. Zoologica 106: 1-106.
- CHITWOOD, B. G. 1932. A synopsis of the nematode parasitic in insects of the family Blattidae. Z. Parasitenkde 5: 14-50.
- Christie, J. R. 1983. A redescription of *Thelastoma robustum* Leidy with comments on other species of the family Thelastomatidae. *Proc. helminth. Soc. Wash.* 5: 65-67.
- COBB, N. A. 1929. Observations on the morphology and physiology of nemas including notes on new species. J. Wash. Acad. Sci. 19: 283-286.
- HUGHES-SCHRADER, S. 1927. Origin and differentiation of the male and female germ cells in the hermaphrodite of *Icerya purchasi* (Coccidae). Z. Zellforsch. 6: 509-540.
- JARRY, D. M. and D. T. JARRY 1968. Tentative de clarification à propos de 60 espèces des genres Cephalobellus et Thelastoma (Nematoda; Oxyuroidea). Annls Parasitol. hum. comp. 43: 339-352.
- Kloss, G. R. 1965. Considerações em tôrno de *Thelastoma* Leidy, 1850 e *Cephalobellus* Cobb, 1920 (Nematoda). *Papeis Dep. Zool. S. Paulo* 17: 131-179.
- Leibersperger, E. 1960. Die Oxyuroidea der europaeischen Arthropoden. *Parasit. Schr Reihe* 11: 1-150.
- Poinar, G. O. 1973. Description and observations on a cuticular infection of *Thelastoma pterygoton* sp. n. (Thelastomatidae; Nematoda) from *Oryctes* spp. (Scarabaeidae; Coleoptera). *Proc. helminth. Soc. Wash.* 40: 37-42.
- Van Waerebeke, D. 1969. Quelques Nématodes parasites de Blattes à Madagascar. *Annls Parasitol. hum. comp.* 44: 761-776.
 - 1970a. Trois nouvelles espèces de Nématodes parasites des Hexodon adultes (Coleoptera; Dynastinae) à Madagascar. Cah. ORSTOM, Sér. Biol. 12: 107-121.
 - 1970b. Deux Oxyures parasites de larves de Lucanidae à Madagascar. Entomophaga 15: 5-14.
 - 1973. Quatre nouvelles espèces d'Oxyuroides associées aux Oryctes à Madagascar. Bull. Mus. nat. Hist. nat. Paris 3º Sér. 123, Zool. 95: 535-553.